

THE POPULATION BIOLOGY OF THE TEMPERATE REEF FISH *CHEILODACTYLUS NIGRIPES* IN AN ARTIFICIAL REEF ENVIRONMENT

by MICHAEL CAPPO*

Summary

CAPPO, M. (1995). The population biology of the temperate reef fish *Cheilodactylus nigripes* in an artificial reef environment *Trans. R. Soc. S. Aust.* 119(3), 113-122, 30 November, 1995.

Underwater surveys and observations of tagged fish were used to examine spatial distribution, temporal variation in abundance, habitat use and agonistic behaviour of a small population of Magpie Perch, *Cheilodactylus nigripes*, in a 1176 m² site beneath a pier over two winters. A marked decline in numbers of small fish in the population was observed in one year and the number of larger fish was more stable. The unstratified density of fish was between 1.6 and 3.4 fish 100 m² but locations of fish sightings were strongly positively correlated with two-dimensional cover of hard substrata within the site. *Cheilodactylus nigripes* was a diurnally active micro-carnivore which used hard substrata for shelter and for feeding on benthic invertebrates. Movement patterns were measured or inferred from spatial patterns of distribution and were found to be restricted to small areas within the confines of the pier. Home range was estimated to be 26 m² for one juvenile fish. Only juveniles ≤ 12 cm TL defended space aggressively against intrusion by conspecifics and fish > 19 cm TL engaged in lateral displays with colour changes in agonistic encounters. These displays were considered to be related to maintenance of spatial patterns.

Replenishment of the pier population was observed to occur in spring from recruitment of 5 cm TL juveniles. These data indicate the importance of relatively small marine protected areas as refuges from spearfishing for *C. nigripes*.

KEY WORDS: temperate reef fish, habitat use, agonistic behaviour, feeding, *Cheilodactylus nigripes*.

Introduction

Cheilodactylid fishes are a numerically important component of the cool temperate reef fish faunas in Australia, New Zealand, South Africa, South America and Japan (Lincoln Smith *et al.* 1989; Branden *et al.* 1986; Leum & Choat 1980; van der Elst 1981; Nielsen 1963; Sano & Moyer 1985). They are relatively large, slow moving and can be easily approached underwater, making them very popular targets for spearfishers. In south-eastern Australia they dominate the catches made in spearfishing competitions (Johnson 1985a; Lincoln Smith *et al.* 1989) and there is evidence that spearfishing is a major cause of localised depletion of cheilodactylids in New Zealand (Cole *et al.* 1990).

Assessment of effects of recreational spearfishing on cheilodactylid populations requires a knowledge of habitat use by the fish, their patterns of movement and abundance and the sources of population replenishment. These data are essential for the implementation of marine protected areas (Edyvane 1993) at the proper spatial scale as a means of managing temperate reef fisheries. A knowledge of feeding habits is also desirable to determine the role of cheilodactylids in trophic dynamics and to predict

any subsequent changes in benthic community structure which may result from the effects of high fishing mortality. Their behavioural traits make these fish ideal subjects for underwater studies yet little is known of the patterns of distribution and ecology of temperate cheilodactylids, especially those that inhabit the coastal reefs of southern Australia.

Cheilodactylus nigripes is an abundant inhabitant of shallow (< 30 metres) limestone and basaltic reefs in southern New South Wales, Victoria, Tasmania, South Australia and southern Western Australia (Hutchins & Swainston 1986). It is commonly found in association with the hard substrata provided by artificial tyre reefs, ship wrecks and piers. This species attains 41 cm in length and rarely takes a baited hook although it comprises a major portion of the spearfishers' catch in South Australia (Johnson 1985a). Limits to the speared catch are enforced by competition bag limits and legislated closure of marine reserves and all piers to spearfishing.

With the exception of counts of *C. nigripes* in surveys of reef faunas in the Great Australian Bight (Kuiter 1983; Branden *et al.* 1986), and frequency in catches at spearfishing competitions (Johnson 1985a,b), there have been no studies of the ecology of this species in Australia.

The present study documents the patterns of spatial and temporal abundance, habitat use and agonistic behaviour in a protected population of *C. nigripes*

* Australian Institute of Marine Science, PMB 3, Townsville MC, Qld, 4810.

below a South Australian pier. Specific aims of the study were to:

- (1) map the spatial and temporal patterns of abundance of the population in relation to the microhabitats provided by the pier,
- (2) describe the feeding morphology and diet of the species and
- (3) describe the agonistic behaviour amongst individuals and its importance in the maintenance of spatial patterns.

Methods

The study site

Edithburgh pier is located on the western side of Gulf St Vincent, South Australia at 35.5°S, 137.45°E (Fig. 1). The seabed below the pier sloped seaward to a maximum depth of approximately 4.5 m at low tide and consisted of a base of coarse sands, gravels and shell. The predominant hard substrata were artificially placed, in the form of fallen pier materials, discarded ship's ballast and debris and a limestone shelf produced

by dredging along the northern side. Large expanses of seagrasses surrounded the structure.

The configuration of pylons and major features of the hard substrata below the pier were mapped (Fig. 2). The entire pier was 168 metres long bounded by 53 rows of timber pylons in 4-5 columns. The study site was under the outer half of the pier seaward of row 23 (Fig. 1). It comprised an area of 1176 m² and was divided into 120 quadrats from 9-11 m² in area with reference to the grid of pylon rows and columns (Fig. 2).

Topographic complexity (Leum & Choat 1980) was described for the site by estimating the two dimensional "cover" of hard substrata within each quadrat, using three ordinal categories of topographic complexity. A total of 804 m² in 81 quadrats was "simple" (cover <= 10%), 225 m² in 24 quadrats had a "middle" level of cover (cover = 11-25%) and 147 m² in 15 quadrats were classified as "complex" (cover > 25%). The seaward end and the southern side of the pier had the most hard substrata, in the form of boulders, slabs and blocks that were usually less than 0.8 m high.

Distribution

Seven visual censuses of the population were made during March-September 1980 using SCUBA. On each census the whole habitat was searched and the position of each fish recorded. The total length (TL) of each fish was estimated to the nearest centimetre and a note was made if the fish were feeding when sighted. Fish were approached to within one metre or less and length estimates were frequently made in direct comparison to a 40 cm plastic ruler. Four censuses of the size frequency under the pier were made by another diver in April-July 1981 and fish lengths were estimated to the nearest centimetre (K. Wehr unpubl. data).

In analyses fish lengths (TL) were categorised as: R recruits (< 6 cm); C1 (6-12 cm); C2 (13-19 cm); C3 (20-26 cm); C4 (> 26 cm). The choice of distinction between C1 and C2 was made to separate young-of-the-year from older fish. These were biologically meaningful divisions of the population, as colour and morphological differences occurred amongst them. The usual colour pattern of *C. nigripes* was three broad, vertical, dark bands on the white background of the body and caudal peduncle and a dark cheek stripe through the eye (Figs 3a, 4a). Recruits had a bright orange caudal fin and pale orange caudal peduncle with black tips on the caudal lobes. The mouth was more terminal than inferior and angled slightly upward giving these fish a shorter snout and deeper chin than larger fish. Size class C1 fish had the same caudal fin colouration but this faded with size to dusky or reddish in larger classes. There were protuberant crests on the preorbital bone of the two largest size classes which were not observed on smaller fish.

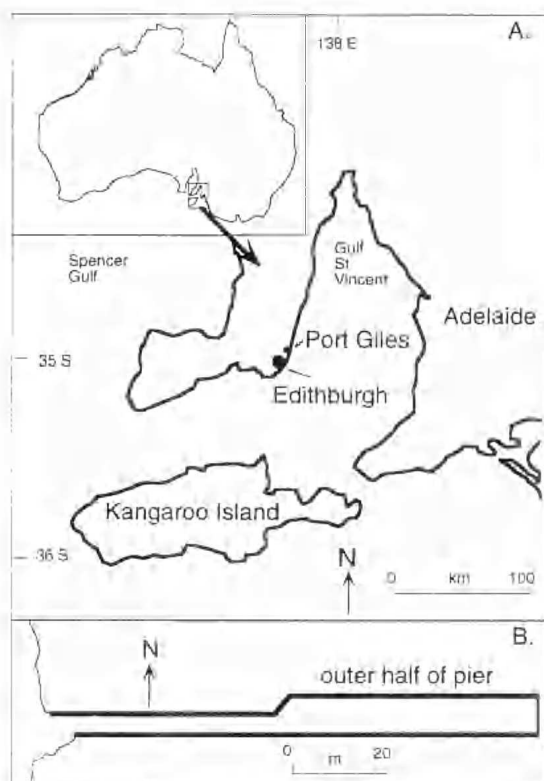


Fig. 1. Location and aspect of Edithburgh pier in Gulf St Vincent, South Australia.

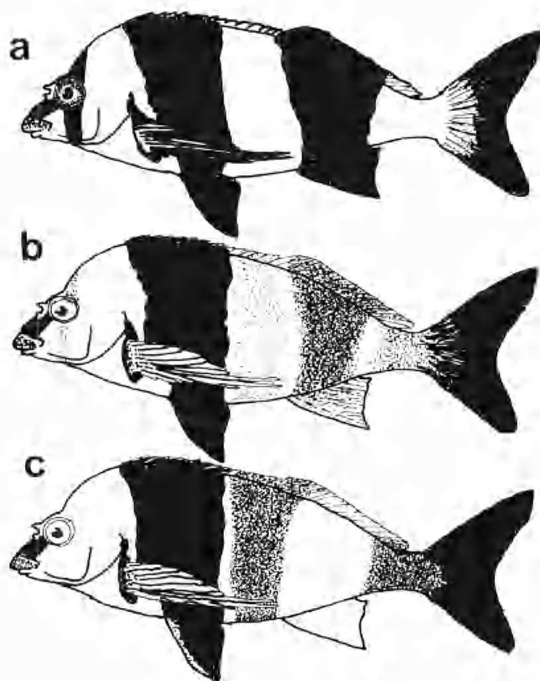
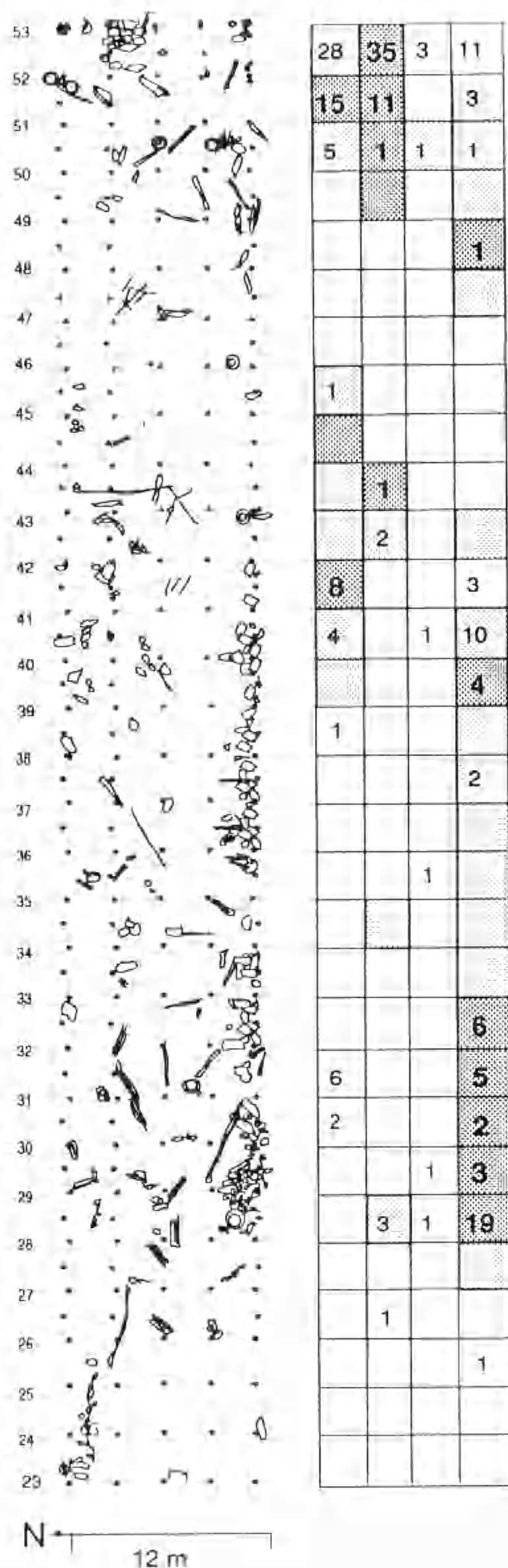


Fig. 3. Summary of colour changes displayed by large *C. nigripes*. a. Normal banding pattern. b. Transitional banding pattern. c. Modified banding pattern - note dark midriff band and caudal peduncle, loss of posterior and cheek bands, white iris and white demarcation between dark bands.

Feeding habits

To avoid sacrificing the small population in the study site a sample of 21 Magpie Perch (TL 21-36 cm) was speared on 25 September 1980 under Port Giles pier 12 km NNE of Edithburgh pier (Fig. 1). Immediately after capture the alimentary tracts were removed and preserved. The food bolus in each tract was dispersed evenly in water and taxa in four field views ($\times 7$) were identified as far as possible. The volume of each taxon in the pooled contents of the alimentary tracts was estimated by a water displacement method.

Observation of movement and behaviour

Underwater behavioural observations were made in 60-minute periods at dawn, midday, dusk and midnight on five days during August-September 1980 from a single vantage point amongst limestone slabs at the seaward end of the pier in pylon row 53 (Fig. 2).

Fig. 2. Comparison of pooled sightings of *C. nigripes* in 1980 and an index of topographic complexity in quadrats (right) with the mapped study site (left). Pylon rows are numbered in ascending order seaward from row 23. "Simple" cover of hard substrata $\leq 10\%$ (no shading); "middle" cover 11-25% (mild shading); "complex" cover $> 25\%$ (dark shading).

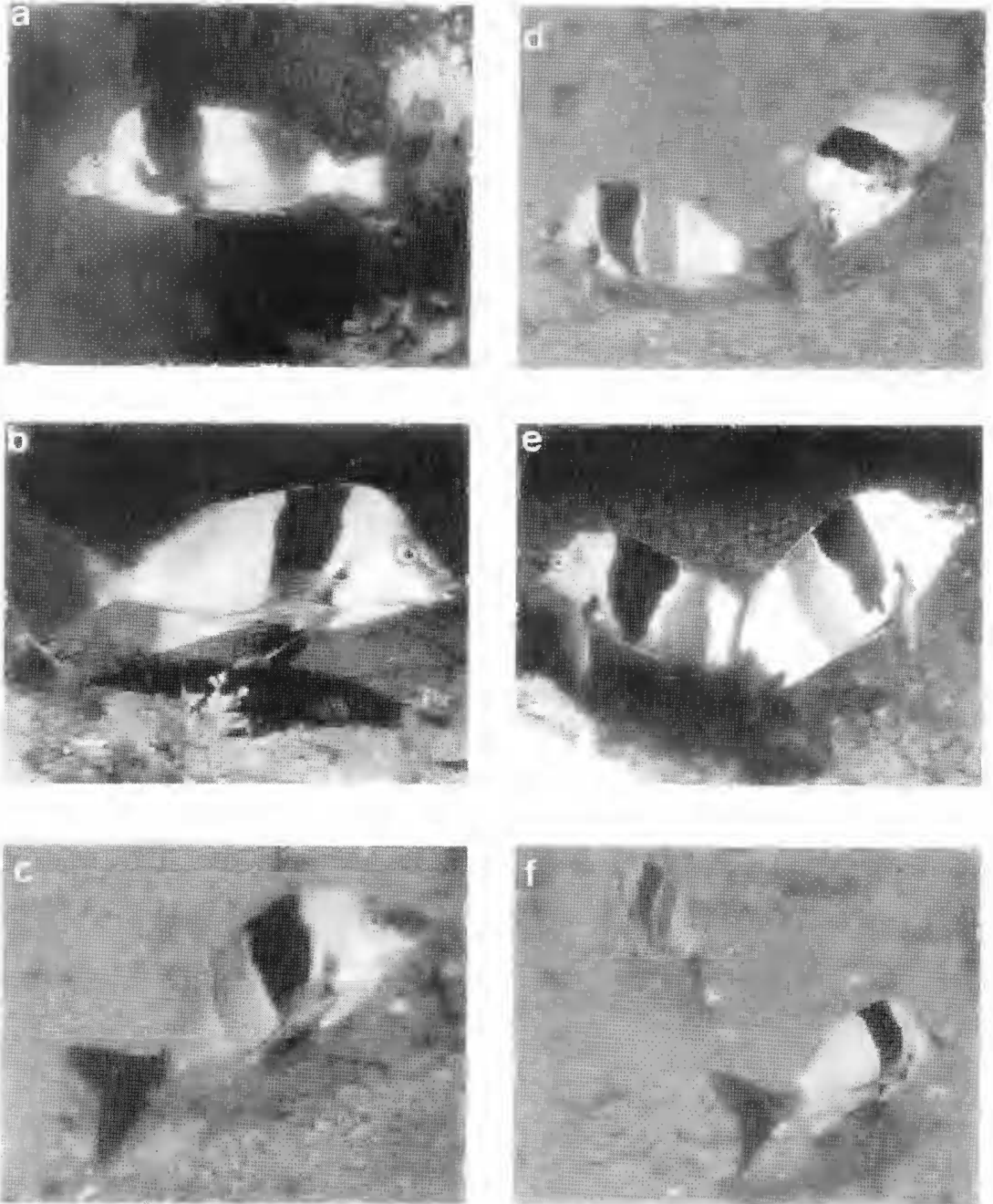


Fig. 4. Photographs of colour change and lateral displays. a. Normal banding pattern. b. Loss of posterior dark band. c. Transitional banding pattern. d. Circling and leaning displays. e. Anti-parallel orientation and modified banding. f. Break in encounter and transitional banding.

Observations began before sunrise and finished after sunset to include crepuscular periods of activity. The movements of four fish at this location were monitored simultaneously during the dawn observation periods. Each fish was recognised individually by tags or body markings. Further observations were made at a variety of locations on an opportunistic basis during 1981-1987.

Data on the movement patterns of tagged individuals were collected during 1980. Seventeen fish were tagged with "T bar" anchor tags individually coded with coloured paints. Fish were captured with a large hand-net, tagged underwater, measured and released immediately at the site of capture, and a numbered stake was used to mark each release site. During subsequent dives the sightings of tagged fish were recorded on the site map. The larger fish in the population evaded capture and the tagged sample (TL 10.5-23.0 cm) did not include C4 fish.

Results

Temporal changes in abundance and size composition

The sightings of fish of the five size classes are shown for each sampling date in Fig. 5. The mean numbers of total sightings for each census were similar for the two years with 29.85 ± 4.30 fish sighted in 1980 (95% CI = 19.32-40.37) and 30.50 ± 1.55 fish in 1981 (95% CI = 25.55-35.44), but seasonal declines in sightings were different.

In 1980 sightings declined from a March high of 53 fish to an August low of 18 (Fig. 5). This was partly

due to the low visibility ($<=0.75$ m) encountered during the August census. The decline was evident for all size classes from March to April when both C1 and C2 declined by one half. The steady decline in C1 numbers may be partly accounted for by growth into the C2 size class which showed an increase in abundance. Recruits were first observed in early September 1980, and increased by late September (Figs 5, 6). Predation may play a role in size-specific mortality as a Southern Calamari squid *Sepioteuthis australis*

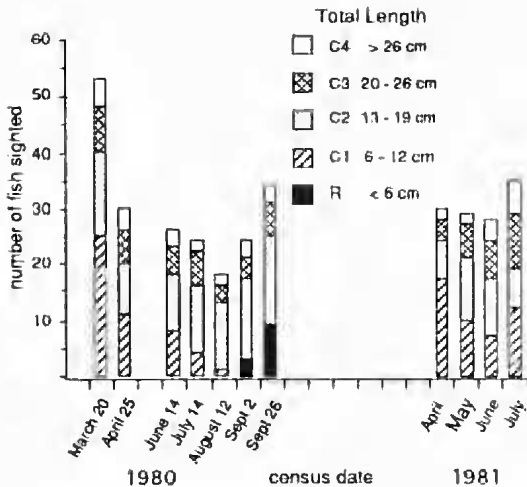


Fig. 5. Changes amongst months in the number of five size classes of *C. nigripes* at Edithburgh pier during 11 underwater visual censuses in 1980 and 1981.

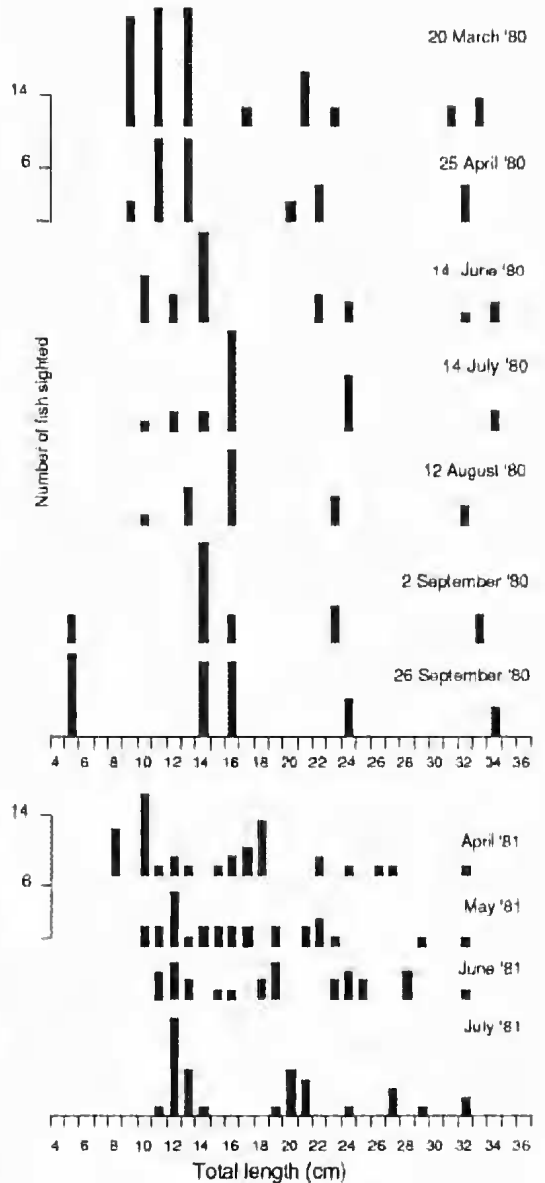


Fig. 6. Modal progression in estimated total length of *C. nigripes* sighted at Edithburgh pier during 1980 and 1981.

was observed to make several attacks on some newly recruited juveniles before capturing and consuming one in 1982.

This pattern was not seen in the 1981 winter surveys although there was a slight decline in the proportion of class C1 fish from April to July. The June low was attributable partly to low visibility (< 0.6 m) encountered during that census. In both years the winter population counts were at comparative levels in the study site. Changes in abundance were relatively small in the two largest size classes amongst months, and between years (Fig. 5). However, the sample sizes and numbers of fish were low, precluding meaningful statistical comparisons. Caution is therefore used in the interpretation of these data.

Modal progression is evident in Fig. 6 for the smaller fish from 1980 to 1981 showing maximum growth rates of about 0.46 cm month⁻¹ for C1 fish and about 0.77 cm month⁻¹ for recruits. These are in general agreement with the measured rate of 0.46 cm month⁻¹ growth of a tagged fish from 13.7 cm to 15.0 cm over five months in 1980. However, the accuracy and precision of length estimation were not determined for either observer so further estimation of growth from modal progression was not possible.

Spatial distribution

The overall density of fish in the study area was estimated at 1.64–3.43 fish per 100 m² in 1980 using 95% confidence limits for the mean number of fish sighted divided by the area surveyed. Localised densities were much higher and the number of *C. nigripes* sighted in quadrats under the pier was positively associated (Spearman $R = 0.5487$, $P = 0.000$) with the amount of hard substrata within quadrats using Spearman's rank correlation procedure (Zar 1984). Fifteen "complex" quadrats comprised only 12.5% of the study area but gave 55% of sightings compared to 30% in "middle" quadrats and only 15% in the remaining 68% of the study area defined as "simple" (Fig. 2). Nearly 18% of all sightings were made in one quadrat on the seaward end of the pier where large limestone slabs and other hard substrata occurred. These slabs were the highest (0.6–1.2 m) and most rugose hard substrata in the study area and provided extensive shelter (Fig. 2). Fish were rarely sighted in quadrats with 10% or less of hard substrata, with the exception of quadrats containing tall three-dimensional structures not well described by the two-dimensional method used to classify quadrats. For example, clusters of buffer pylons on the seaward corners of the pier were fused together by encrusting organisms and provided shelter sites.

There was no clear relationship between water depth and fish size due to the shallow nature of the habitat and the overriding influence of three-dimensional reef structure. However, the largest fish were generally

restricted to the deepest water and were not seen in the area shoreward of pier row 51 (Fig. 2). New recruits were seen throughout the study area, but mainly near the sea surface on pylons at the deepest seaward end, amongst arborescent bryozoans.

Movement of fish in the study area

Observations throughout the day and in the night showed that individual *C. nigripes* emerged from shelter sites just after dawn and retreated to the same sites during sunset. No fish were seen to be active at night. In five night dives two of the largest fish in the population were seen in the same shelter site in a crevice between close pylons, resting motionless on outstretched pectoral fins with raised spinous dorsal fins. It appeared that largest fish emerged earlier and retreated later than smaller size classes. The movements of three fish were monitored in each of the five dawn observation periods but the fourth and smallest (C1) fish was only seen for the first three days. The largest fish (C4) traversed an average of 8.0 ± 1.0 metres, a 23.0 cm tagged fish moved 7.8 ± 0.37 metres and a 14.0 cm tagged fish moved 2.5 ± 0.55 metres in the 60 minutes after emergence from their individual shelter sites. The smallest individual moved only 0.83 ± 0.28 metres. Only the largest fish moved far from the confines of the pier, foraging amongst low limestone shelves within 10 metres of the seaward end.

Seven of the tags (41%) were not seen after application, three others persisted for only 9 days, and only five tags were sighted after 60 days. The movement of large Magpie Perch could not be assessed from the tagging program because the mean length at release for these remaining five fish was only 15.4 cm (C1, C2) and the largest was 23.0 cm (C3). Only four tagged fish were present at the end of the 1980 study period and each of these fish was seen during every census following tagging. The loss of tags from the population was at least partly due to tag shedding. On two occasions fish were observed to scrub the tag off against hard objects. The sightings of all tagged fish were restricted to the habitat underneath the pier within 7 metres of the tagging site with the exception of two individuals. Several weeks after tagging these two fish were found to be resident for the remainder of the study in quadrats about 10 metres away from the tagging site. Tagged fish were never seen to traverse the seagrass beds on the southern side of the pier which appeared to act as natural boundaries to the pier habitat.

Wilson (1975) defined "home range" to be the area that an animal learns thoroughly and habitually patrols, and "core area" to be the area of heaviest regular use within the home range. Only a single tagged fish was seen frequently enough to confidently estimate these two areas. This small C2 fish (13.7 cm) was sighted 18 times within 7 metres of the tagging site. The home range of this fish was estimated to be only 26 m² by measuring the area of a polygon joining the outermost

sightings (Leum & Choat 1980). Similarly, the core area was estimated at 1.7 m² to be the area encompassing 50% of sightings. The focus of this area was a small shelter site within a cavern amongst limestone blocks on the southern side of the pier in pylon row number 28 (Fig. 2). This fish was only sighted once outside the shaded confines of the pier and the furthest displacements were northward under the pier and westward along the pylons.

Feeding morphology and diet

Cheilodactylus nigripes had a small mouth with thick fleshy lips and a single row of widely spaced peg-like teeth on the dentary and premaxillary. In the throat there were a pair of upper, and a single lower, pharyngeal tooth pads covered with bands of villiform teeth. There were 15 long and fine gillrakers on the first gill arch and the stomach was small with a large pyloric region containing five short pyloric caeca.

The fish were observed to inspect closely pockets of sediment in crevices or amongst fronds of arborescent organisms and fed in a pecking motion. The mouth was rapidly opened, forming a suction with the fleshy lips, and benthos was ingested with an audible clicking sound. By rapidly opening and closing the opercula, fine silt was strained out through the gill chambers and larger particles were ejected from the mouth. Large polychaetes were wrenched from the substratum and vigorously shaken to break them up into pieces suitable for swallowing. When close observations were made, no evidence of prey was seen near the fish and they appeared to select feeding substrata, but not the benthic organisms within, although fish directed repeated feeding "pecks" at large prey such as polychaetes once they were detected.

The fish fed mainly on benthic invertebrate fauna with gammarid amphipods about 4 mm long predominant in the pooled sample. Of the 60% of food volume identifiable, the fourteen major taxa were ranked as: gammarids (25.6%); Polychaeta (10%); ostracods (7.5%); Bivalvia (6.6%); Brachyura (3.2%); Mysidacea (2.7%); and Tanaidacea, Archaeogastropoda, Polyplacophora, Gastropoda, Isopoda, Ophiuroidea, and caprellid and tubicolous amphipods (each less than 1%).

There did not appear to be any size-related difference in the feeding behaviour of *C. nigripes* with the exception that small fish were observed to feed more often than larger ones. Of all sightings made in 1980 the following proportions were engaged in feeding when sighted: R 75%; C1 76%; C2 79%; C3 49%; C4 45%.

Agonistic behaviour

Wilson (1975) defined agonistic behaviour to be any activity related to fighting, whether aggression or conciliation and retreat. Agonistic behaviour in *C. nigripes* was directed toward only conspecifics of a

similar size and three size-specific patterns were described for the smallest and largest size classes.

The smallest fish (<=12 cm), classified as recruits (R) and C1, aggressively defended space. Most common was a short pursuit of incoming R or C1 fish away from a foraging area. Also observed was the head-on approach of C1 fish to within about 4 cm followed by sustained pursuit, darting in small circles with the dorsal fin fully raised. Biting was evident as audible sounds and tail damage from broken caudal rays. This was termed "carousel fighting" by Chiszar (1978).

Three slow lateral display patterns were observed amongst fish more than about 19 cm long (C3, C4) which did not involve such pursuit. The first involved pairs of C3 fish which approached each other head-on and met head-to-tail in a parallel orientation, often within centimetres, and one or both fish tilted upward slowly. The two fish then swam in slow circles in close proximity with some lateral displays, but no colour change, before parting.

An elaboration of this theme occurred during the approach of the large C4 fish when a characteristic colour change occurred. The posterior band began to pale and the white midriff darkened with the development of a sharp white line between them (Figs 3b,c, 4c,d). When the fish met they assumed an anti-parallel orientation separated by only a few centimetres for about 15 seconds, during which they slowly tilted 30 degrees to a head-up, tail-down position (Fig. 4e). The posterior band blanched and the darkening of the midriff and caudal peduncle deepened. Other colour changes were also striking, including blanching of the anal fin, cheek band, iris and pectoral fins, and definition of a black patch around the pectoral axil (Fig. 3b,c). When one fish withdrew the other followed and both began lateral "leaning displays" with lowered or raised dorsal spines, described by Chiszar (1978) as defensive posturing (Fig. 4d). The entire sequence lasted one to two minutes and once the fish broke off the encounter the midriff band quickly resumed its former white state but the other bands were slower to return (Fig. 4c,f).

These displays were clearly identified to occur when fish met and appeared to relate to the position of the fish within the habitat, although it was not possible to define the home ranges and spatial boundaries involved in eliciting the agonistic behaviour. The significance of a third type of behaviour was more obscure and involved the loose aggregation of large fish into a slowly circling group above the seabed. Most of the circling fish had a pale posterior band and some of the fish exhibited a leaning display towards others. There was insufficient information to recognise characteristics of "winners" or "losers" and no attempt was made to identify the sex of the participants, but these lateral displays were considered to relate to habitat use.

Discussion

The low variability in counts of *C. nigripes* amongst most months in winters of two years, the very close association between fish sightings and topographic complexity and the restricted movements of tagged fish were all evidence for a high degree of site specificity of *C. nigripes* under the Edithburgh pier. Rugosé, hard substrata were used as sleeping and sheltering sites and as feeding substrata and the concept of a small home range may best describe the use of this space by *C. nigripes*.

These patterns of habitat use indicate that relatively small artificial habitats such as piers can act as important marine protected areas for this species. Marine protected areas can fulfill a number of important functions in fisheries management including protection of "critical habitats" and provision of areas for stock replenishment, for fishery-independent monitoring of stock fluctuations and for resolution of conflict amongst competitors for use of marine resources and habitats. (Edyvane 1993). Planning the spatial scale and habitat composition of marine protected areas for temperate reef fishes requires knowledge of sources of population replenishment, ontogenetic movement patterns, home range size, habitat requirements and natural habitat boundaries. Some of these can be inferred for *C. nigripes* from the simple observations presented here supported by comparison with other detailed studies of the cheilodactylids associated with reefs.

Distribution and movement

In translation of the pier observations to natural reef populations of *C. nigripes* in South Australia it is essential to recognise that major biological features of the habitat have been shown to affect the distribution of temperate reef fish at a variety of spatial scales and these patterns have been maintained over long time scales (Jones 1988; McCormick 1989b). In this regard the artificial nature of the pier habitat is considered to differ from nearby natural reefs in two main ways. Unlike the algal-dominated reefs surveyed by Branden *et al.* (1986), the habitat beneath Edithburgh pier lacked macrophyte cover, perhaps because of shading. There may thus be more suitable feeding substrata there for *C. nigripes*, as Choat & Ayling (1987) found that larger carnivorous reef fishes, including cheilodactylids, forage preferentially in open reef areas which support greater densities of their invertebrate prey in comparison to areas dominated by laminarian algae. The amount of habitat for feeding and refuge is further enhanced under the pier by the presence of the pylons and the fouling communities that encrust them. Secondly, the density of *C. nigripes* beneath the pier (1.6-3.4 per 100 m²) was six-fold higher than an estimate for unexploited reefs of the Great Australian Bight (0.2 - 0.6 per 100 m²) calculated from the survey data in Branden *et al.* (1986). The home range

sizes, movement patterns and agonistic behaviour on natural reefs may be different as a consequence.

The microhabitat requirements of *C. nigripes* for shelter sites and feeding substrata were not described with the simple habitat classifications used here but can be determined by studying associations between abundance and habitat at small spatial scales. McCormick & Choat (1987) stratified estimates of density of the morwong *Cheilodactylus spectabilis* in New Zealand, by ten habitat types and depth, and reported averages of 0.25-2.09 fish per 100 m², with the exception of the topographically complex "tumble boulderbank" habitat where the density was 15.87 fish per 100 m².

There is also a clear role for ontogenetic movements along environmental gradients in establishing patterns of cheilodactylid abundance and these should be considered in selection of reef areas for protection. After first recruiting in surge zones (Leum & Choat 1980) cheilodactylids are known to move to progressively deeper parts of the reef habitat as they grow (Sano & Moyer 1985; McCormick 1989a,b). Although the seagrass beds around the pier appeared to act as habitat boundaries which smaller *C. nigripes* did not traverse, it was not possible to describe immigration and emigration of fish with the simple techniques used in the study. Replenishment of the pier population was observed to occur only through the spring arrival of new recruits.

The autumn decline in numbers of these young-of-the-year in 1980 was not observed in 1981 censuses, and it was not possible to resolve the roles of size-specific natural mortality, tag-induced mortality or counting biases in the decline of such a small population. Properly replicated censuses stratified to identify individual fish and detect counting biases and diurnal and seasonal differences in activity, would help clarify these temporal changes. The pier map and census data presented here provide a baseline for future surveys to examine long-term variations in patterns of abundance of *C. nigripes* at Edithburgh.

It is possible that home ranges and movements on natural reefs may be more extensive amongst all size-classes of *C. nigripes*, and it is unknown whether the distributions reported here were more, or less, restricted during warmer months outside the study period. Leum & Choat (1980) attributed significant winter declines in numbers of *C. spectabilis* sighted to an extension of home range during cooler months. The estimates of home range for *C. nigripes* were relatively small in comparison to those constructed for *C. spectabilis* by Leum & Choat (1980) on natural reefs and may depend on fish density as well as habitat type. Juvenile *C. spectabilis* had home ranges ≤ 100 m², which were about three times that estimated here for *C. nigripes* using the same technique. Similarly the largest *C. nigripes* were always sighted in a relatively

small area at the seaward end of the Edithburgh pier but Leum & Choat (1980) observed that larger *C. spectabilis* moved large distances and had home ranges up to 50-70 thousand m².

Feeding habits

Cheilodactylus nigripes were diurnally active, benthic carnivores feeding mainly on gammaridean amphipods and other small benthic invertebrates. Their mode of feeding is common to other reef-associated morwongs in the same genus. Bell (1979) reported that *C. fuscus* and *C. spectabilis* use their thick fleshy lips to wrench and suck animals off the substratum, mainly polychaetes, brachyurans, amphipods, gastropods, and bivalves. Sano & Moyer (1985) reported that the Japanese *C. zebra* feeds mainly on epifauna, especially gammaridean amphipods and decapods, while the sympatric *C. zonatus* tends to take both epifauna (mainly gammaridean amphipods, isopods, sponges and decapods) and infaunal polychaetes.

Agonistic behaviour

Juvenile *C. nigripes* < 12 cm TL were observed to defend space aggressively, but such defence may have been energetically uneconomical for larger fish > 19 cm TL occupying larger home ranges. It is proposed here that the lateral displays and colour-change during agonistic encounters amongst larger *C. nigripes* were related to the maintenance of some undefined spatial pattern of overlapping home ranges. Such patterns were mapped by Leum & Choat (1980) for *C. spectabilis* which directed agonistic behaviour only towards conspecifics of similar size and only smaller size classes vigorously defended space outside of the spawning season. The habitat of *C. spectabilis* was described as a mosaic of exclusive territories occupied by smaller fish through which the larger size classes foraged in larger, overlapping home ranges (Leum & Choat 1980) and this may be a useful model for future studies of habitat use by *C. nigripes*.

Using Chiszar's (1978) definitions of lateral displays in agonistic behaviour, the description of "curious fighting" fits well the behaviour of *C. nigripes* juveniles, whereas the various colour phases of larger fish can be interpreted as varying degrees of threat in a typical "colour fight". The anti-parallel orientation adopted during these reciprocal lateral displays is widespread in fishes, and some species with long dorsal spines, such as the chaetodontids, are reported to tilt the raised spines towards the other fish in a defensive posture called "rolling" or "leaning" if it approaches too closely (Chiszar 1978).

The possibility of a reproductive basis for some agonistic behaviours cannot be discounted for all observations of *C. nigripes*, as McCormick (1989a) found that large male *C. spectabilis* aggressively defended territories during the spawning season by "rolling" down on to intruders and restrained visiting

females by "tight circling, pursuit and blocking" or chasing and tail-nipping. Some of the larger *C. nigripes* at Edithburgh pier were observed to have tentacular protuberances on the preorbital bones which have been used in studying sexual dimorphism and separating the sexes of *C. spectabilis* and *C. fuscus* by external characters in visual counts (McCormick 1989a; Schroeder *et al.* 1994). The high population densities of *C. nigripes* at some deeper South Australian piers may provide the best chances of clarifying the spatial and sexual significance of agonistic behaviour of *C. nigripes* through observation and morphometric studies.

Future research

The resilience of *C. nigripes* to spearfishing and recovery of depleted populations depend on growth rates and the sources and rate of population replenishment. This study suggests that widespread movement of *C. nigripes* amongst habitats is not an important source of replenishment but further studies at appropriate scales are necessary to determine the contributions of recruitment and post-recruitment processes in determining spatial patterns of abundance. These data are needed to determine if marine protected areas should include shoreline surge zones as recruitment sites with corridors of hard substrata linking them to adjacent deeper reef, or if isolated offshore habitats such as artificial reefs are adequate.

The magnitude and frequency of changes in population structure are likely to be directly related to the longevity of *C. nigripes* as variable recruitment will have least effect and spearfishing the greatest effect on the population size of long lived species. When fishing mortality is absent in such cases age classes accumulate and temporal consistency in population size may mask an underlying instability in the age composition (Jones 1988). Consequently, future studies of *C. nigripes* population dynamics may require analyses of age compositions of unexploited populations in conjunction with recruitment surveys (Doherty & Fowler 1994) and monitoring of the survival, growth and movement of individually recognisable fish from time of recruitment in permanent quadrats (Connell & Jones 1991). The results presented here form a basis for such studies and for longer-term assessment of temporal consistency in the patterns of abundance of *C. nigripes* in a mapped habitat.

Acknowledgments

Most of this study was undertaken whilst the author was a BSc(Hons) student in the Department of Zoology, University of Adelaide. A. J. Butler provided supervision, logistic and financial support and use of the Coobowie Marine Research Station. The author also gratefully acknowledges the contributions of K. Wehn for use of unpublished data, C. Proctor and A.

Davis for assistance with diving and revision of the pier map, and M. Keough, K. Branden and K. Handley for photography. The comments of M. McCormick,

I. Suthers, D. Booth and especially two anonymous reviewers greatly improved earlier drafts of the manuscript.

References

- BELL, J. D. (1979) Observations on the diet of Red Morwong, *Cheilodactylus fuscus* Castelnau (Pisces: Cheilodactylidae). *Aust. J. Mar. Freshw. Res.* **30**, 129-133.
- BRANDEN, K. L., EDGAR, G. J., & SHEPHERD, S. A. (1986) Reef fish populations of the Investigator Group, South Australia: a comparison of two census methods. *Trans. R. Soc. S. Aust.* **110**(2), 69-76.
- CHISZAR, D. (1978) Lateral displays in the lower vertebrates: forms, functions, and origins p. 320. In Reese, E. S. & Lighter, F. J. (Eds) "Contrasts in behaviour: Adaptations in the aquatic and terrestrial environments." (Wiley and Sons, New York).
- CHOAT, J. H. & AYLING, A. M. (1987) The relationship between habitat structure and fish faunas on New Zealand reefs. *J. Exp. Mar. Biol. Ecol.* **110**, 257-284.
- COLE, R. G., AYLING, T. M. & CREESE, R. G. (1990) Effects of marine reserve protection at Goat Island, northern New Zealand. *N.Z. J. Mar. Freshw. Res.* **24**, 197-210.
- CONNELL, S. D. & JONES, G. P. (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *J. Exp. Mar. Biol. Ecol.* **151**, 271-294.
- DOHERTY, P. J. & FOWLER, A. J. (1994) An empirical test of recruitment limitation in a coral reef fish. *Science* **263**, 935-939.
- EIDYVANE, K. S. (1993) An ecosystem-based approach to marine fisheries management pp. 21-27. In Hancock, D. A. (Ed.) "Sustainable fisheries through sustaining fish habitat. Australian Society for Fish Biology Workshop. Victor Harbor, SA, 12-13 August, Bureau of Resource Sciences Proceedings." (Aust. Govt Publ. Service, Canberra).
- VAN DER ELST, R. (1981) "A guide to the common sea fishes of southern Africa." (C. Strunk Publishers, Cape Town).
- HUTCHINS, B. & SWAINSTON, R. (1986) "Sea fishes of Southern Australia." (Swainston Publishing, Perth).
- JOHNSON, J. E. (1985a) Spearfishing competitions in South Australia (1983/84). 1. Shore and boat events. *Fish. Res. Pap. Dep. Fish. (S. Aust.)* **12**, 1-17.
- _____ (1985b) Spearfishing competitions in South Australia (1983/84). 2. Australian skindiving convention. *Ibid.* **14**, 1-15.
- JONES, G. P. (1988) Ecology of rocky reef fish of north-eastern New Zealand: a review. *N.Z. J. Mar. Freshw. Res.* **22**, 445-462.
- KUITER, R. (1983) An annotated list of fishes of the Investigator Group, South Australia. *Fish. Res. Pap. Dep. Fish. (S. Aust.)* **7**, 1-12.
- LÉUM, L. L., & CHOAT, J. H. (1980) Density and distribution patterns of the temperate marine fish *Cheilodactylus spectabilis* (Cheilodactylidae) in a reef environment. *Marine Biology* **57**, 327-337.
- LINCOLN SMITH, M. P., BELL, J. D., POLLARD, D. A. & RUSSELL, B. C. (1989) Catch and effort of competition spearfishermen in Southeastern Australia. *Fisheries Research* **8**(1989), 45-61.
- MCCORMICK, M. I. (1989a) Reproductive ecology of the temperate reef fish *Cheilodactylus spectabilis* (Pisces: Cheilodactylidae). *Mar. Ecol. Progr. Ser.* **55**, 113-120.
- _____ (1989b) Spatio-temporal patterns in the abundance and population structure of a large temperate reef fish. *Ibid.* **53**, 215-225.
- _____ & CHOAT, J. H. (1987) Estimating total abundance of a large temperate-reef fish using visual strip-transects. *Marine Biology* **96**, 469-478.
- NIELSEN, J. G. (1963) On the development of *Cheilodactylus variegatus* Valenciennes 1833 (Cheilodactylidae). *Copeia* **1963**, 528-533.
- SANO, M. & MOYER, J. T. (1985) Bathymetric distribution and feeding habits of two sympatric Cheilodactylid fishes at Miyake-jima, Japan. *Jap. J. Ichthyol.* **32**(2), 239-247.
- SCHROEDER, A., LOWRY, M. & SUTHERS, I. (1994) Sexual dimorphism in the Red Morwong, *Cheilodactylus fuscus*. *Aust. J. Mar. Freshw. Res.* **45**(7), 1173-1180.
- WILSON, E. O. (1975) "Sociobiology. The new synthesis." (Harvard University Press, Cambridge, Massachusetts).
- ZAR, J. H. (1984) "Biostatistical analysis." (Prentice-Hall, New Jersey).